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Quick Minds Don't Blink: Electrophysiological Correlates of Individual Differences in Attentional Selection

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Abstract

■ A well-established phenomenon in the study of attention is the attentional blink—a deficit in reporting the second of two targets when it occurs 200–500 msec after the first. Although the effect has been shown to be robust in a variety of task conditions, not every individual participant shows the effect. We measured electroencephalographic activity for ''nonblinkers'' and ''blinkers'' during execution of a task in which two letters had to be detected in an sequential stream of digit distractors. Nonblinkers showed an earlier P3 peak, suggesting that they are quicker to consolidate information than are blinkers. Differences in frontal selection positivity were also found, such that nonblinkers showed a larger difference between target and distractor activation than did blinkers. Nonblinkers seem to extract target information better than blinkers do, allowing them to reject distractors more easily and leaving sufficient resources available to report both targets. ■

INTRODUCTION

Conscious awareness presupposes several interrelated processes, including sensory preprocessing by modality-specific cortical circuits, attentional selection by frontoparietal networks, and transfer of the results of selection into working memory (Kranczioch, Debener, Schwarzbach, Goebel, & Engel, 2005; Rees, Kreiman, & Koch, 2002). Some of these processes are assumed to work in parallel and may handle almost unlimited amounts of information. However, the capacity of working memory is known to be severely limited (e.g., Linden et al., 2003; Cowan, 2001; Luck & Vogel, 1997), making it important to select only that information that is most relevant to current goals and intentions. Attention should not be paid to irrelevant information, thus curtailing processing and preventing it from reaching awareness and competing with relevant information. The more efficient an individual is in ignoring irrelevant information, the more relevant information he or she will be able to take up and remember. However, not everyone is equally capable of selecting relevant from irrelevant information, and large individual differences exist in the amount of concurrently presented information that people can become aware of (e.g., Johnson & Proctor, 2004).

Here, we use the paradigm of the attentional blink (AB) to study individual differences in the dynamics of attention and awareness over time, and we record electroencephalographic (EEG) activity to pinpoint the neural correlates from which these individual differences may arise. By systematically varying the lag between two successive targets embedded within a rapid serial visual presentation (RSVP) stream of distractors, the time course of selecting and attending these targets can be measured (e.g., Duncan, Ward, & Shapiro, 1997; Raymond, Shapiro, & Arnell, 1992). The AB is a deficit in reporting the second target (T2) when it occurs 200–500 msec after the first (T1), presumably due to difficulty in consolidating T2 in working memory (Martens, Wolters, & van Raamsdonk, 2002; Rolke, Heil, Streb, & Henninghausen, 2001; Vogel, Luck, & Shapiro, 1998; Luck, Vogel, & Shapiro, 1996). Electrophysiological data indicate that during an AB, T2 fails to evoke the P3 potential associated with working memory updating, whereas it still elicits event-related potentials (ERPs) associated with visual and semantic processing (P1, N1, and N400). Not only has the AB proven to be robust in a variety of task conditions, the effect is also resistant to training (Braun, 1998).

A number of studies have previously reported variations in the duration and magnitude of the AB. For instance, a prolonged AB has been found not only in patients with lesions in the inferior parietal lobe, superior temporal gyrus (Shapiro, Hillstrom, & Husain, 2002), and frontopolar cortex (Rizzo, Akutsu, & Dawson, 2001), but also in dyslexics (Hari, Valta, & Uutela, 1999), people with attention-deficit hyperactivity disorder (Hollingsworth, McAuliffe, & Knowlton, 2001), and the elderly (Lahar, Isaak, & McArthur, 2001). Interestingly,

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some exogenous and endogenous control over the allocation of attentional resources seems possible, as the magnitude of the AB is known to be reduced when, for instance, the participant's own name is presented as one of the targets (Shapiro, Caldwell, & Sorensen, 1997), when participants are concurrently engaged in a distracting mental activity such as listening to music (Olivers & Nieuwenhuis, 2005), or when a cue is provided as to when the targets will appear (Martens & Johnson, 2005).

An aspect of the AB that up till now has been largely ignored is that the magnitude of the AB varies from one individual to another. Whereas some participants show decrements in T2 performance of 80% of baseline performance or more, others show no measurable AB. Given that the AB is widely assumed to reflect fundamental limitations in information processing, an intriguing question is why the latter group of people, which we will refer to as ''nonblinkers,'' do not show an AB. Understanding this may also improve our understanding as to why and how the AB normally does occur.

To our knowledge, only one study has reported and compared blinkers and nonblinkers (Feinstein, Stein, Castillo, & Paulus, 2004). In an event-related functional magnetic resonance imaging (fMRI) study, Feinstein et al. (2004) investigated the AB by contrasting the brain activity of eight blinkers with that of eight nonblinkers and found that nonblinkers showed more activity than did blinkers in the anterior cingulate (Brodmann's area [BA] 32), medial prefrontal cortex (BA 9), and frontopolar cortex (BA 10). The anterior cingulate has been suggested to be involved in decisions between conflicting response tendencies (Turken & Swick, 1999), the medial prefrontal cortex seems to be engaged whenever we attend to our own mental states or the mental states of others (for a review, see Frith & Frith, 2003), and the frontopolar cortex is assumed to be involved whenever the results of subgoal processing need to be integrated with the information stored in working memory (Braver & Bongiolatti, 2002). In addition, frontopolar activation has been correlated with the participant's level of preparation (Dreher, Koechlin, Ali, & Grafman, 2002). Involvement of these areas reflect the task requirements in an AB paradigm: Incoming stimuli have to be matched to an internal description of each target (medial prefrontal cortex); the subgoals of identifying two targets have to be maintained while a rapid stream of distractors is viewed, updating working memory when targets are detected (frontopolar cortex); and decisions have to be made regarding which actions should be taken in response to the perceived targets (anterior cingulate). Other neuroimaging studies on the AB (not distinguishing between blinkers and nonblinkers) have also suggested general involvement of a fronto–parieto–temporal attentional network incorporating the brain areas described by Feinstein et al. (2004) (e.g., Hommel et al., in press; Kranczioch et al., 2005; Marois, Yi, & Chun, 2004). It is an intriguing question whether this fronto–parieto–temporal attentional network may function more efficiently in some people (e.g., nonblinkers) than in others (e.g., blinkers).

With respect to this question, the findings of Feinstein et al. (2004) are interesting, but it remains unclear whether the differences in activation they found for blinkers and nonblinkers reflect individual differences or task-related differences. That is, the differences in target-related prefrontal activity may have been observed because nonblinkers often identified T2s, whereas the blinkers often missed T2s. What is currently missing is detailed temporal information about brain activity when blinkers and nonblinkers are performing an AB task. Not only does EEG provide a time resolution that is much better than that of event-related fMRI; by examining the presence or absence of several well-studied ERP components, additional information can be obtained about the distinct cognitive processes involved. Therefore, we investigated individual differences in the AB by measuring EEG brain activity in blinkers and nonblinkers, and examined components of the ERP that have been linked to the selective processing of target features (frontal selection positivity [FSP] and selection negativity [SN]) and working memory updating (P3). By comparing the peak latencies of the P3s induced by successfully identified T1s and T2s, one can determine whether nonblinkers consolidate visual information faster than blinkers do. By investigating components (the FSP and SN) associated with the selective processing of target features, one can determine whether nonblinkers are more efficient in selecting targets from nontargets than are blinkers.

This approach might not only help to elucidate how individuals differ in the way attentional resources are allocated across time, but it might also allow a test of theoretical models of the AB. Two leading models of the AB are the *two-stage model*, originally proposed by Chun and Potter (1995), and the *interference model*, proposed by Shapiro, Arnell, and Raymond (1997) and Shapiro, Raymond, and Arnell (1994). According to the two-stage model, stimuli are processed to the point of conceptual representation during the first stage, which is assumed to have an unlimited capacity. During the second stage, limited-capacity attentional processes are needed to consolidate representations into a durable and reportable form. The AB arises when T1 consumes the majority of the attentional resources, preventing the consolidation of T2. In the interference model, the selection of information for access to working memory is based on a matching process that determines whether a particular item matches the target description (cf. Duncan & Humphreys, 1989). Items meeting the target criteria gain entry into visual short-term memory (VSTM) and are assigned a selection weight. The probability of successful selection for report from VSTM depends on the number and similarity of items in VSTM: The more

items and the greater their similarity to each other, the lower the probability of correct retrieval.

A major difference between the two-stage model of Chun and Potter (1995) and the interference model of Shapiro et al. (1994) is that the two-stage model assumes that T2 fails to reach working memory because of its vulnerability to interference or decay while still in Stage 1, whereas the interference model assumes that both T1 and T2 may reach VSTM (Stage 2), but that T2 may be lost due to interference with T1 or distractors. If nonblinkers are more efficient in selecting relevant targets from irrelevant nontargets, the interference model would predict differences between nonblinkers and blinkers in EEG components related to selective target processing (the FSP and SN), as well as differences in the amount of EEG activity induced by the irrelevant nontargets. The two-stage model makes no clear prediction about differences in target selection processes, but certainly does not predict differences in the amount of distractor-related frontal EEG activity because this activity is assumed to reflect processing beyond Stage 1, and, according to the model, nontargets are not processed beyond Stage 1. A finding that nonblinkers process visual information and consolidate targets faster than do blinkers, would be consistent with both models and should be reflected in the latency of P3s induced by identified targets. However, the interference model predicts that the consolidation of both targets will be slowed when presented at a short lag (due to mutual interference within VSTM), whereas the two-stage model predicts slowing of the consolidation of only T2 because T2 must wait for limited-capacity consolidation processes to be freed.

To summarize, we predict that there will be differences in processing speed (reflected by differences in P3 peak latencies) between blinkers and nonblinkers. Second, differences in selective target processing (reflected by the FSP and SN components) are expected. Third, according to the interference model, differences in the amount of distractor-related EEG activity can be expected.

EXPERIMENT 1

Methods

Participants

Participants were selected on the basis of their performance in previous AB experiments performed in our laboratory. Out of 207 participants in former experiments (see, e.g., Martens, Elmallah, London, & Johnson, in press; Nieuwenstein, Johnson, Martens, & Kanai, submitted; Martens & Johnson, 2005), 16 participants showed little or no AB. These individuals, whom we will refer to as nonblinkers, were retested to ensure that the observed lack of an AB effect was consistent across experiments and testing sessions. The AB task consisted of identifying two letters in an RSVP stream of digits, each item presented for 90 msec. T2 was the first, third, or eighth item following T1 (i.e., it was presented at Lag 1, 3, or 8, respectively).

AB magnitude was computed according to the following formula: {[(T1 accuracy at Lag 2 − T2|T1 accuracy at Lag 2) / T1 accuracy at Lag 2] + [(T1 accuracy at Lag 3 − T2|T1 accuracy at Lag 3) / T1 accuracy at Lag 3] / 2} × 100. Of the 16 nonblinkers, 14 also showed an AB magnitude of less than 10% in the screening test and, thus, were selected for the present experiment. From the pool of 207 participants, 14 additional participants who showed an AB magnitude of at least 20% were selected. For both groups of participants, an additional selection criterion was that T1 accuracy had to be 80% or better.

All participants were recruited from the University of Groningen community, had normal or corrected-to-normal visual acuity and no history of neurological problems. Three nonblinkers reported being left-handed. Informed consent was obtained prior to the experiment, and participants received payment of €7 per hour.

Stimuli and Apparatus

The generation of stimuli and the collection of responses were controlled by using E-prime 1.1 software (Schneider, Eschman, & Zuccolotto, 2002) running under Windows 2000 on a PC with a 1.5-Ghz processor. Stimuli were digits (excluding 1 and 0) and consonants (excluding "Q" and "Y"), subtending 0.3° by 0.4° of visual angle at a viewing distance of approximately 80 cm. The stimuli were presented in black (2 cd/m^2) on a white background (88 cd/m^2) presented in 14-point Courier New font on a 17-in. monitor.

Procedure

The experiment consisted of a practice block of 24 trials and four experimental blocks of 144 trials each. At the start of each block, 12 additional warm-up trials were provided that were not included in the analyses. A short break was given after each block, and a longer break (approximately 15 min) was given halfway through the experiment.

Before each trial, a fixation cross was presented in the middle of the screen. After 1024 msec, a message appeared at the bottom of the screen, prompting participants to press the space bar to initiate the trial. When the space bar was pressed, the message disappeared immediately. The fixation cross remained on the screen for 500 msec, followed by the RSVP stream consisting of 20 stimuli. Each item in the stream was presented for 90 msec at the center of the screen. In two thirds of the trials, two target letters were embedded in the stream (dual-target trials), in one sixth of the trials only one

target letter was present (single-target trials), and in one sixth of the trials, no targets were present (no-target trials). In dual- and single-target trials, T1 was always presented as the fifth item in the stream. In dual-target trials, T2 was the first, second, third, or eighth item following T1 (i.e., it was presented at Lag 1, 2, 3, or 8, respectively). These specific lags were chosen on the basis of the literature and previous work in our laboratory. For blinkers, T2 is likely to be ''blinked'' (i.e., not identified) at Lags 2 and 3, whereas little or no reduction in T2 accuracy is usually observed at Lags 1 and 8. Target letters were randomly selected with the constraint that T1 and T2 were always different letters. Digit distractors were randomly selected with the constraint that no single digit was presented twice in succession.

To minimize possible eye blink and movement artifacts in the EEG at the end of the stream, the fixation cross reappeared in the middle of the screen for 1024 msec at the end of the RSVP stream. Subsequently, participants were prompted by a message at the bottom of the screen to type the letters they had seen using the corresponding keys on the computer keyboard. Participants were instructed to take sufficient time in making their responses to ensure that typing errors were not made. If a letter was not seen, the space bar was to be pressed instead. Participants were encouraged to type in their responses in the order in which the letters had been presented, but responses were accepted and counted correct in either order. Before, after, and halfway through the experiment, baseline EEG activity was measured while participants relaxed for 1 min with eyes opened and 1 min with eyes closed. Participants completed the task in approximately 135 min (including the breaks).

EEG Recording

EEG activity was recorded from tin electrodes mounted on a 64-channel elastic electrocap organized according to the international 10/20 system and connected to a 64-channel head box (Twente Medical Systems, Enschede, the Netherlands). Electrode impedance was reduced to less than 5 kΩ. The signal was referenced against electrodes on the earlobes, and an electrode on the sternum was used as a common reference. The 62 scalp electrodes used were FP1, FPZ, FP2, AF7, AF3, AFZ, AF4, AF8, F7, F5, F3, FZ, F4, F6, F8, FT9, FC5, FC3, FC1, FCZ, FC2, FC4, FC6, FT10, T7, C5, C3, C1, CZ, C2, C4, C6, T8, CP5, CP3, CPZ, CP4, CP6, P9, P7, P5, P3, P1, PZ, P2, P4, P6, P8, P10, PO3, POZ, PO4, PO7, O1, OZ, O2, PO8, PO9, O9, LZ, O10, and PO10. In the final analyses, only the signals from Pz (central parietal), F7 (left frontal), F8 (right frontal), PO7 (left parieto-occipital), and PO8 (right parieto-occipital) were used. The other electrodes were used to obtain a clear scalp distribution of the various components to ensure the accurate detection of the relevant waveforms (the P3, FSP, and SN, respectively). The horizontal electrooculogram (EOG) was recorded from tin electrodes attached approximately 1 to 2 cm to the left and right of the outside corner of each eye. The vertical EOG was recorded from two tin electrodes attached approximately 3 cm below the left eye and 1 cm above the brow of the left eye, respectively. EEG data were recorded by using Brain Vision Recorder (Brain Products GmbH, Munich, Germany) running under Windows 2000 on a separate PC with a 1.5-Ghz processor. The EEG signal was sampled with a frequency of 2 kHz. Later, the sampling frequency was digitally reduced to 250 Hz.

Data Analysis

The data were analyzed by using Brain Vision Analyzer (Brain Products). The ERPs were time locked to the onset of the RSVP stream, had a duration of 1800 msec, and were calculated relative to a 200-msec prestream baseline, yielding a total length of 2 sec. The ERP segments were 20-Hz low-pass filtered, corrected for eye movements, DC detrended (to remove direct current drift artifacts), and baseline corrected before artifact rejection was applied. Segments with maximum differences of values greater than 100 μV (i.e., containing artifacts) were excluded from further analysis (a total of 12.8% of the trials, ranging from 2% to 60%, $SD = 13.13$, of the trials per participant). For one participant, more than 30% of the trials were lost due to artifacts. As this nonblinker showed good performance for T1, a clear lack of an AB effect, and clear target-induced P3 components, he was included in the analyses.

Analyses were restricted to 11 blinkers (mean age 20.4 years, 4 women) and 11 nonblinkers (mean age 21.5 years, 4 women) who continued to fulfill the selection criteria for blinkers and nonblinkers as described in the Participants section. Three nonblinkers who were excluded showed an AB magnitude that was greater than 10% (10.2%, 12.0%, and 17.9%), and three blinkers were excluded because AB magnitude dropped below 20% (17.5%, 13.8%, and 2.4%). None of the included participants changed groups.

Because of overlapping waveforms due to the temporal proximity of targets presented at Lags 1 and 2, analyses of the ERPs from dual-target trials were restricted to Lags 3 and 8. Where appropriate, Greenhouse–Geisser-corrected p values are reported.

Behavioral Results and Discussion

T1 performance in the single-target condition of the AB task was better for nonblinkers (96.7%) than for blinkers (91.5%), $t(20) = 2.97$, $SE = 1.78$, $p = .008$. Figure 1A shows T1 performance in the dual-target condition as a function of lag for blinkers and nonblinkers. A repeated measures analysis of variance (ANOVA) with group

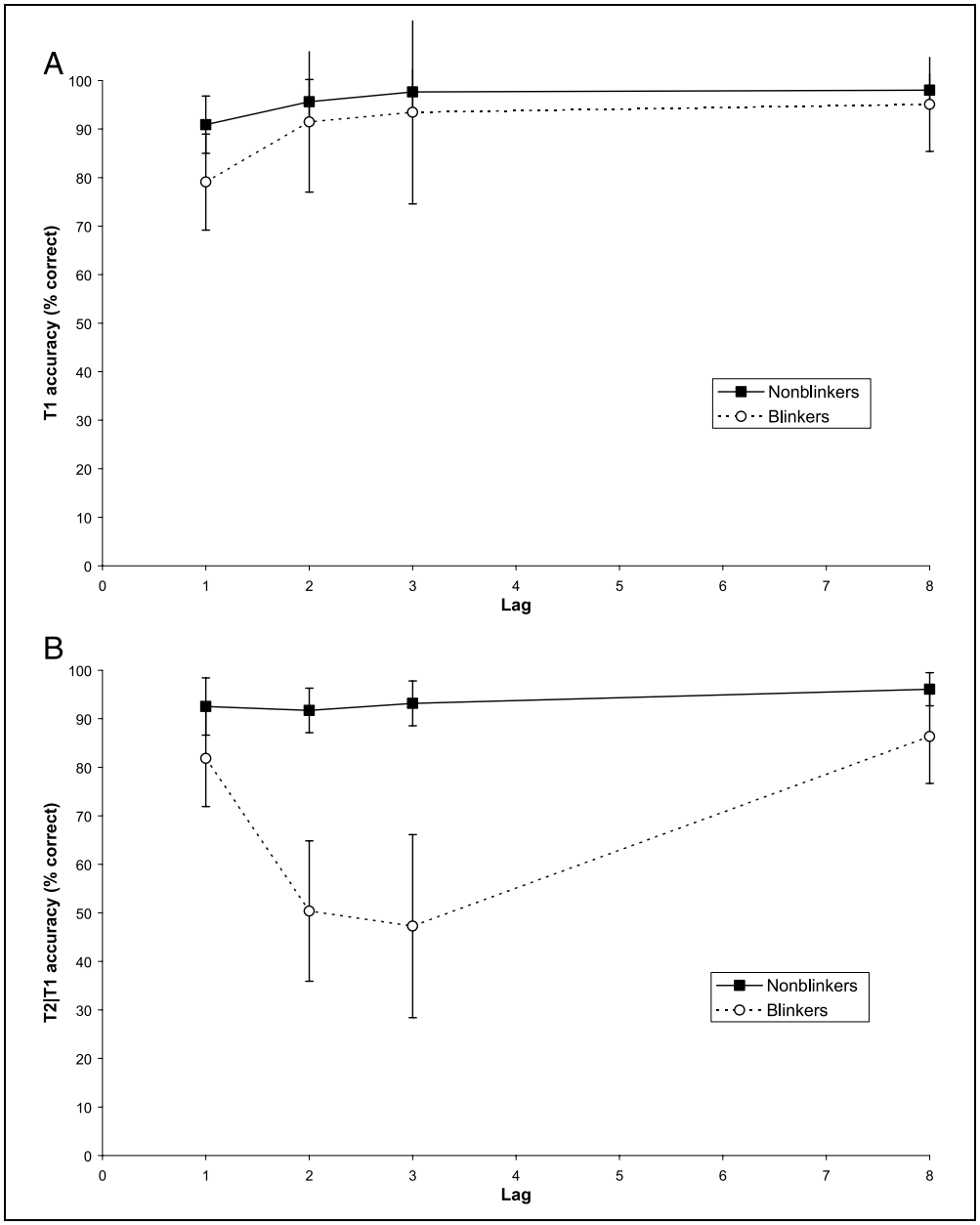

Figure 1. (A) Mean percentage correct report of T1 as a function of lag, for nonblinkers (solid line) and blinkers (dotted line). (B) Mean percentage correct report of T2, given correct report of T1, as a function of lag, for nonblinkers (solid line) and blinkers (dotted line). Error bars reflect standard deviation.

(nonblinkers or blinkers) as a between-subjects factor and lag (1, 2, 3, or 8) as a within-subjects factor revealed significant effects of group, $F(1,20) = 7.80$, $MSE = 93.98$, $p = .011$, and lag, $F(3,60) = 23.26$, $MSE = 26.13$, $p < .001$. In addition, a significant Group × Lag interaction was found, $F(3,60) = 3.50$, $MSE = 26.13$, $p = .047$, suggesting that the decrement in T1 performance at Lag 1 was greater for blinkers than for nonblinkers.

Figure 1B shows performance for T2 on those trials for which T1 was reported correctly (T2|T1), as a function of lag for each group. An ANOVA with group (nonblinkers or blinkers) as a between-subjects factor and lag (1, 2, 3, or 8) as a within-subjects factor revealed significant main effects of group, $F(1,20) = 65.40$, $MSE = 244.01$, $p < .001$, and lag, $F(3,60) = 43.42$, $MSE = 59.67$, $p < .001$. A significant Group × Lag interaction was also found, $F(3,60) = 34.63$, $MSE = 59.67$, $p < .001$, reflecting that only blinkers showed an AB.

Neurophysiological Results and Discussion

Baseline EEG Activity

To ensure that any differences in activation between blinkers and nonblinkers were not due to a priori differences in EEG activity, mean EEG activity was measured while participants relaxed, 1 min with eyes opened and 1 min with eyes closed, before, after, and halfway through the experiment. In addition, mean EEG activity was also examined from a 1024-msec period

during which a fixation point was displayed, at the start of each trial. No significant differences in mean EEG amplitude were found between the two groups for electrodes F7, F8, PO7, PO8, or Pz during these periods ($ps > .12$). In addition, no significant differences were found between the two groups when the mean EEG activity within specific frequency bands (alpha, beta, theta, or delta) was examined ($ps > .13$).

The P3

A well-known hallmark of the AB is that targets that are successfully identified induce a P3, whereas no P3 is typically found for a ''blinked'' (i.e., an incorrectly reported or missed) T2 (e.g., Martens et al., in press; Kranczioch, Debener, & Engel, 2003; Vogel et al., 1998). Because the P3 component is generally maximal at parietal sites, the signal from the Pz electrode was used for all analyses of the P3. Figure 2A shows the ERPs for blinkers on no-target trials, nonblink trials (i.e., trials in the Lag 3 condition in which both T1 and T2 were correctly identified), and blink trials (i.e., trials in the Lag 3 condition in which T1 was correctly identified and T2 was not correctly identified), respectively. Visual inspection of Figure 2 shows a lack of a P3 in no-target trials and a clear T1-related

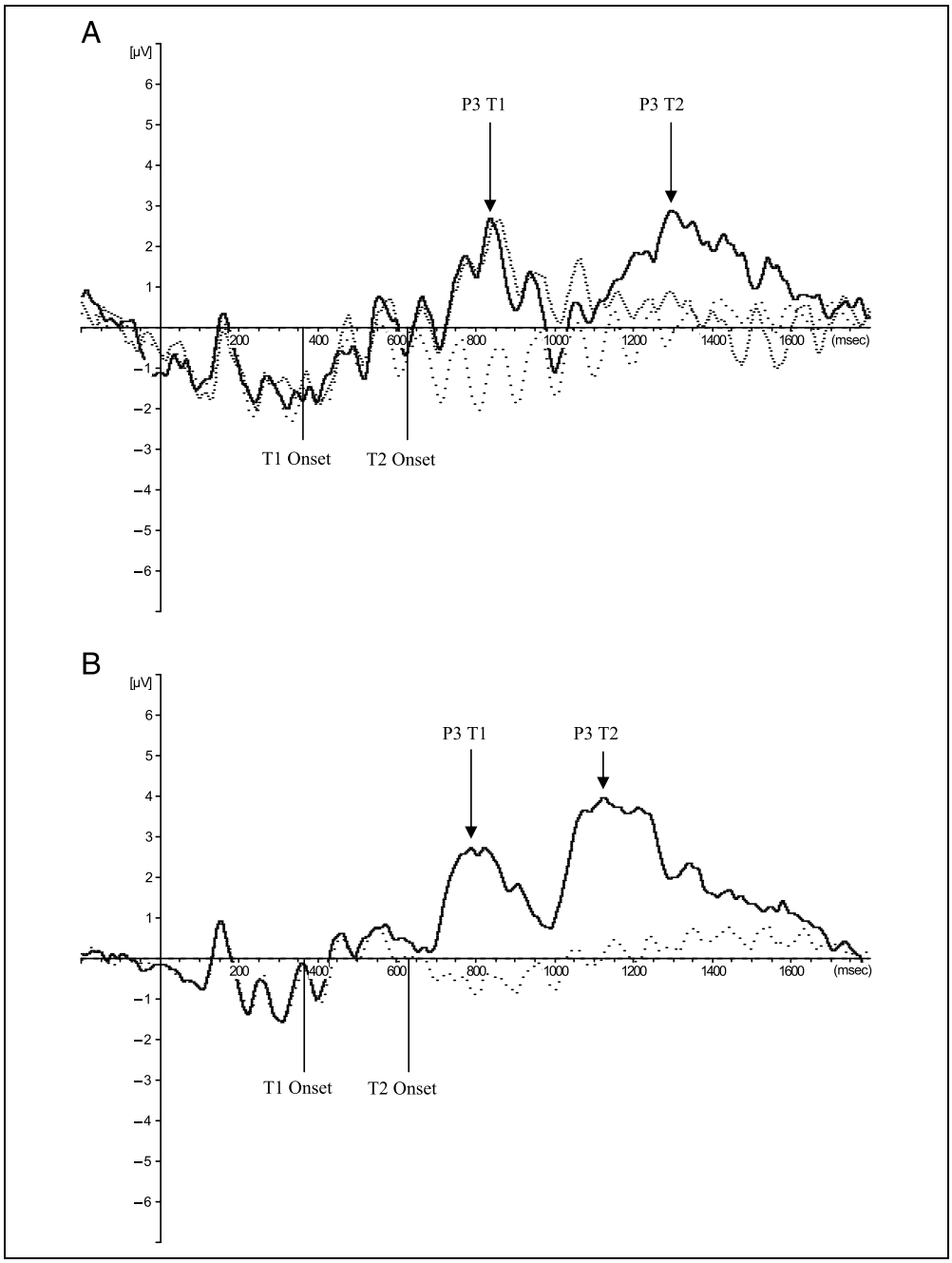

Figure 2. Grand averages of the mean activation at Pz of blinkers (A) and nonblinkers (B) as a function of time for Lag 3 trials during which an AB did not occur (no-blink trials, solid line), Lag 3 trials during which an AB did occur (blink trials, densely dotted line), and trials during which no targets were presented (no-target trials, dotted line). ERPs were time locked to the onset of the RSVP stream.

P3 response in both blink and nonblink trials, consistent with the idea that the P3 reflects target consolidation, in this case of T1. In addition, a T2-related P3 response was present in nonblink trials and was absent in blink trials, which is in line with previous findings (e.g., Martens et al., in press; Kranczioch et al., 2003).

Figure 2B shows the ERPs for nonblinkers on no-target trials and nonblink trials. Blink trials are not presented because, by definition, nonblinkers rarely show an AB, making a meaningful analysis of these results impossible. On nonblink trials, two clear P3 peaks can be distinguished, induced by T1 and T2, respectively, whereas no P3 component was present in no-target trials.

The Latency of the P3

One potential explanation for the behavioral difference between blinkers and nonblinkers might be that the two groups differ in the speed of information processing. To test this hypothesis, the latencies of the P3 peaks on nonblink trials at Lags 3 and 8 were examined. Figure 3 shows the P3s induced by the two identified targets for nonblinkers and blinkers on nonblink trials at Lag 3 (A) and Lag 8 (B). For both T1 and T2, at both Lag 3 and

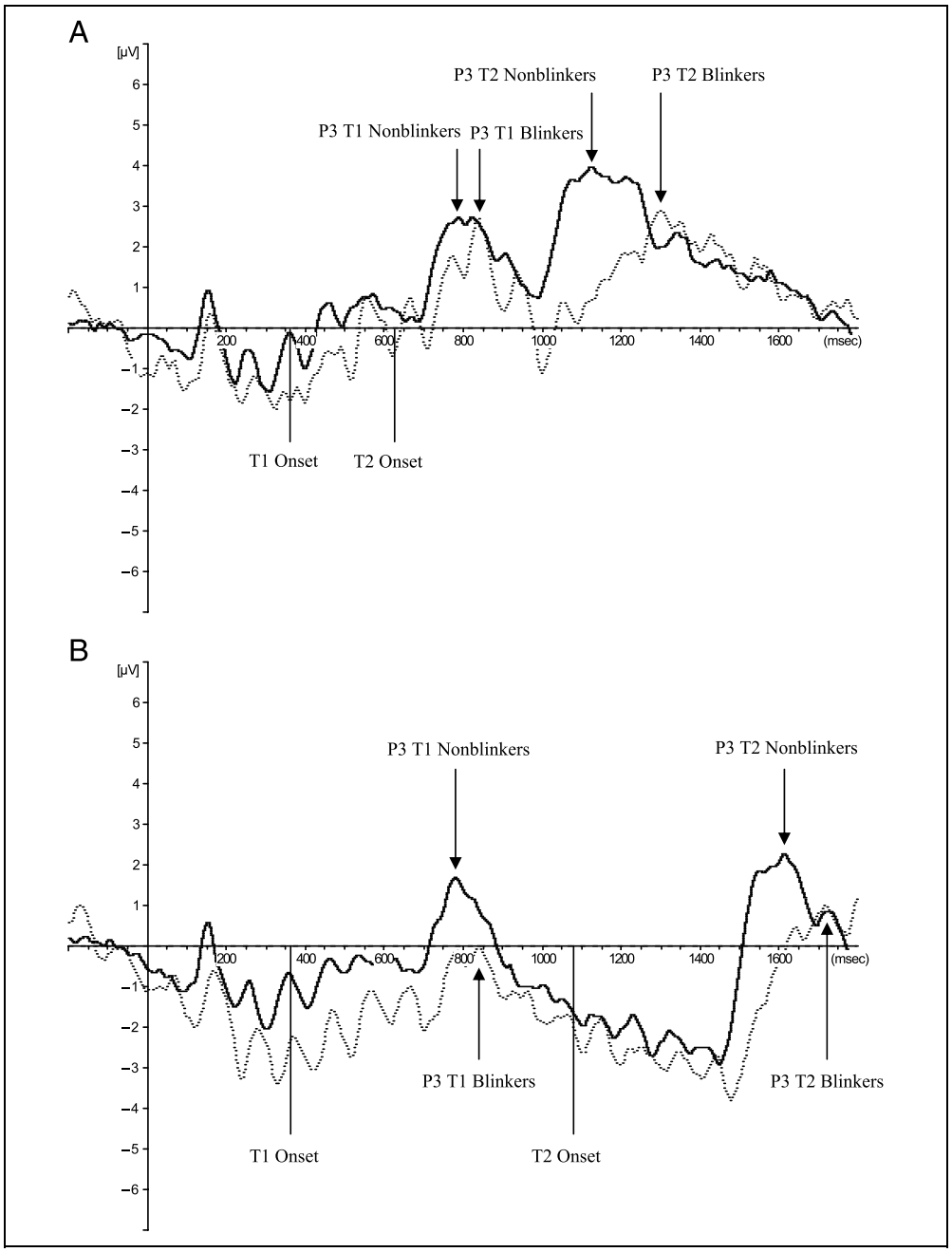

Figure 3. Grand averages of the mean activation at Pz of nonblinkers (solid line) and blinkers (densely dotted line) as a function of time for Lag 3 trials (A) and Lag 8 trials (B) during which an AB did not occur (no-blink trials). ERPs were time locked to the onset of the RSVP stream.

Lag 8, nonblinkers seem to show an earlier P3 peak than blinkers do, suggesting that nonblinkers are able to identify targets more rapidly, which may lead to an earlier consolidation of relevant information. The mean time required to consolidate a target, referred to as ''consolidation latency,'' was calculated for each participant by subtracting the onset time of the target (relative to the beginning of the stream) from the mean latency of the P3 peak evoked by it. The resulting consolidation latencies were averaged across participants and are presented in Table 1. A repeated measures ANOVA with group as a between-subjects factor (blinkers or nonblinkers) and lag (3 or 8) and target (T1 or T2) as within-subject factors revealed significant main effects of group, $F(1,20) = 25.14$, $MSE = 5300.44$, $p < .001$, lag, $F(1,20) = 10.64$, $MSE = 4532.22$, $p = .004$, and target, $F(1,20) = 122.30$, $MSE = 4121.31$, $p < .001$. In addition, a significant Group × Target interaction was found, $F(1,20) = 6.30$, $MSE = 4121.31$, $p = .021$. Although blinkers seemed to be slower to consolidate both T1 and T2, the differences in consolidation latency between blinkers and nonblinkers were larger for T2 than for T1. None of the other interactions were significant ($ps > .17$). Separate independent t tests performed on T1 and T2 across lags showed that blinkers were indeed slower than nonblinkers to consolidate both T1, $t(20) = 2.22$, $p = .019$ (one-tailed), and T2, $t(20) = 5.16$, $p < .001$ (one-tailed). It is somewhat surprising that the delay in consolidating targets at Lag 3 relative to Lag 8 (the Lag 3 consolidation delay) was essentially the same for both targets (for blinkers, these differences were 68 and 66 msec for T1 and T2, respectively, and for nonblinkers these differences were 25 and 28 msec, respectively).

Target Selection: The FSP and the SN

Given that the nonblinkers were faster to consolidate targets than blinkers, two ERP components were examined that have been associated with the selective processing of target features: the FSP and the SN components. The FSP and SN amplitudes in response to T1 were determined by subtracting distractor-related activity from target-related activity at the electrodes where FSP and SN activity is generally found to be maximal (F7 and F8 for the FSP and PO7 and PO8 for the SN; see, e.g., Smid, Jakob, & Heinze, 1999). For each individual, target-related activity was measured by taking the peak FSP and SN amplitudes evoked by T1s that were successfully identified on either single- or dual-target trials, within a window of 180–340 msec after the onset of T1. Distractor activity was measured by taking the amplitude of the ERP signal, in no-target trials, at the same latency as the target-related FSP or SN peak.

Table 1. Mean Consolidation Latency (Milliseconds) of T1 and T2 in Nonblink Trials as a Function of Lag for Blinkers and Nonblinkers (Standard Deviation in Parentheses)

	T1		*T2*	
Group	*Lag 3*	*Lag 8*	*Lag 3*	*Lag 8*
Blinkers	495 (60.9)	427 (72.4)	680 (80.3)	614 (56.6)
Nonblinkers	430 (57.2)	405 (57.3)	549 (81.1)	521 (52.9)

Separate analyses were conducted for frontal (FSP) and parieto-occipital (SN) activity in the brain due to different polarities of the components. For the frontal electrodes, a repeated measures ANOVA with group (nonblinkers or blinkers) as a between-subjects factor and trial type (target or no target), hemisphere (left or right), and condition (single or dual target) as within-subject factors revealed a significant main effect of trial type, $F(1,20) = 59.00$, $MSE = .71$, $p < .001$, indicating the presence of a significant FSP. In addition, a significant Trial Type × Group interaction was found, $F(1,20) = 10.00$, $MSE = .71$, $p = .005$, such that the nonblinkers showed a larger FSP (see Figure 5, top) than did blinkers (see Figure 4, top). No other main effects or interactions were found ($ps > .10$). For the parieto-occipital electrodes, a significant main effect of trial type was found, $F(1,20) = 57.07$, $MSE = 2.58$, $p < .001$, indicating the presence of a significant SN. In addition, a significant Trial Type × Hemisphere interaction was found, $F(1,20) = 8.98$, $MSE = 1.65$, $p = .007$. No other main effects or interactions were significant ($ps > .09$). The Trial Type × Hemisphere interaction was such that the difference between target and no-target activity was greater at PO7 than at PO8, a pattern of activity that is in line with the literature (e.g., Hillyard & Münte, 1984). Note, however, that no Trial Type × Group interaction was found for the parieto-occipital electrodes, indicating that blinkers (see Figure 4, bottom) and nonblinkers (see Figure 5, bottom) did not significantly differ in SN amplitude.

Separate preplanned ANOVAs were conducted for the frontal and parieto-occipital regions with trial type (target or no target), hemisphere (left or right) and condition (single or dual target) as within-subject factors. For blinkers, significant main effects of trial type, $F(1,10) = 18.86$, $MSE = .39$, $p = .001$, and condition, $F(1,10) = 6.22$, $MSE = .26$, $p = .03$, were revealed, such that a significant FSP was present, with more frontal activity in dual-target than in single-target trials. In addition, a significant Trial Type × Hemisphere interaction was found, $F(1,10) = 6.55$, $MSE = .45$, $p = .03$, such that the FSP was larger in the left (see Figure 4, top left) than in the right hemisphere (see Figure 4, top right). For nonblinkers, only a significant main effect of trial type was found, $F(1,10) = 40.31$, $MSE = 1.04$, $p < .001$, reflecting the presence of a bilateral FSP (see Figure 5, top). No other main effects or interactions were found for the blinkers or nonblinkers. For the parieto-occipital region, only the main effect of trial type was significant for the nonblinkers, $F(1,10) = 26.25$, $MSE = 4.29$,

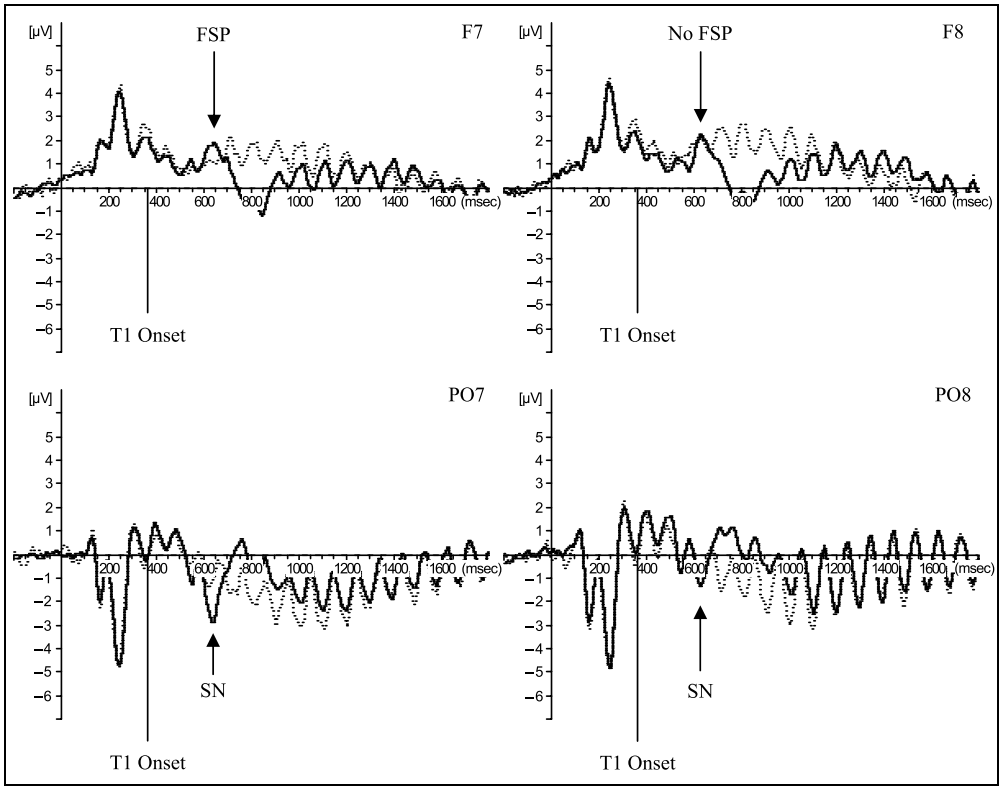

Figure 4. Grand averages of the mean activation at F7, F8, PO7, and PO8 of blinkers as a function of time for target trials (solid line) and no-target trials (densely dotted line). ERPs were time locked to the onset of the RSVP stream.

$p < .001$, reflecting the presence of a bilateral SN (see Figure 5, bottom). For the blinkers, however, not only was the main effect of trial type significant, $F(1,10) = 49.25$, $MSE = .87$, $p < .001$, there was also a significant Trial Type × Hemisphere interaction, $F(1,10) = 14.24$, $MSE = .66$, $p = .004$, such that the SN was larger in the left (see Figure 4, bottom left) than in the right hemisphere (see Figure 4, bottom right). No other main

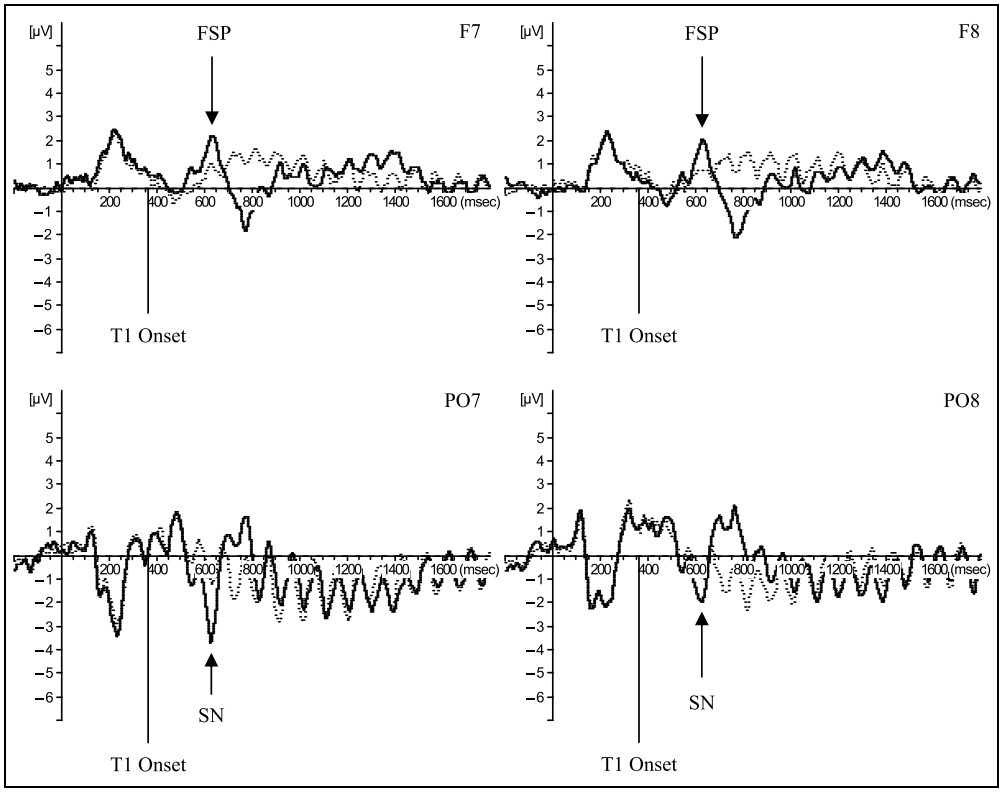

Figure 5. Grand averages of the mean activation at F7, F8, PO7, and PO8 of nonblinkers as a function of time for target trials (solid line) and no-target trials (densely dotted line). ERPs were time locked to the onset of the RSVP stream.

effects or interactions were found for the blinkers or nonblinkers.

Possible differences in FSP and SN peak latencies were also examined. Repeated measures ANOVAs with group (nonblinkers or blinkers) as a between-subjects factor and hemisphere (left or right) and condition (single or dual target) as within-subject factors revealed no significant main effects or interactions for the frontal regions (concerning the FSP; ps $> .12$) nor for the parieto-occipital regions (concerning the SN; ps $> .14$).

We conclude that for nonblinkers a clear bilateral FSP was present, whereas for the blinkers only a small FSP could be discerned in the left hemisphere (F7) and little or no FSP in the right hemisphere (F8). In contrast, a comparable SN was found for both blinkers and nonblinkers in the parieto-occipital region (although for the blinkers it was significantly stronger in the left than in the right hemisphere).

In an additional analysis, FSP difference scores on blink and no-blink trials were compared for blinkers to investigate whether an FSP can also be found for blinkers on trials during which they successfully identify both targets (no-blink trials). However, paired samples t tests showed no significant differences between blink and nonblink trials at F7 or F8 (ps $> .10$), suggesting that blinkers consistently show little or no FSP over the right prefrontal cortex.

Correlations between Early Target-related Activity and AB Magnitude

The differential EEG activity that was found in blinkers and nonblinkers suggests that the selective processing of the targets associated with such activity might play a crucial role in determining whether an AB will or will not occur. If so, it might be possible to predict whether an individual is likely to show a strong AB on the basis of the amount of target selection activity induced by T1. Pearson product–moment correlations were computed between individual AB magnitudes and the absolute difference between target- and distractor-related activity for electrodes PO7, PO8, F7, and F8. A significant negative correlation was found between target-related activity at F8 and the magnitude of the AB, $r = -.45$, $p = .036$ (two-tailed). In an additional analysis, we included only blinkers, as the range of AB magnitude values was, by definition, restricted for the nonblinkers. A significant negative correlation was again found for F8, $r = -.57$, $p = .033$ (one-tailed). In addition, a significant negative correlation was found for PO7, $r = -.58$, $p = .030$ (one-tailed).

Differences in Distractor-related Mean EEG Activity

Support for the hypothesis that nonblinkers are more efficient than blinkers in selecting targets from distractors, is provided by analyses of no-target trials. Figure 6 shows the ERPs of trials during which only distractors were presented for electrodes F7, F8, Pz, PO7, and PO8, respectively. Blinkers seem to show more distractor-related EEG activity than nonblinkers do, especially at the electrodes located above the lateral prefrontal cortex (F7 and F8; see, e.g., Smid et al., 1999; Passingham, 1993). Independent-samples t tests conducted on the mean activity during the presentation of the RSVP stream (i.e., the mean amplitude over the entire ERP segment) for each of the electrodes F7, F8, Pz, PO7, and PO8 showed a significant difference between blinkers and nonblinkers for electrode F8, $t(20) = 2.37$, $SE = .27$, $p = .014$ (one-tailed), but not for the other electrodes (ps $> .11$).

As can be seen in Figure 6 (top), the two lines representing the distractor activity of blinkers and nonblinkers seem to converge about 1200 msec after the onset of the RSVP stream, the time after which no more targets should be expected within the RSVP stream (i.e., post Lag 8). t Tests restricted to this time window (0–1200 msec) showed a significant difference between blinkers and nonblinkers for F8, $t(20) = 3.04$, $SE = .33$, $p = .003$ (one-tailed), and a marginally significant difference for F7, $t(20) = 1.51$, $SE = .46$, $p = .074$ (one-tailed). No significant differences were found for the other electrodes (all other ps $> .16$). The increased activation in response to each distractor in the interval during which targets can be expected shown by blinkers relative to nonblinkers suggests that they have more trouble distinguishing targets from distractors at an early stage of processing.

As can be seen in Figure 6, blinkers also showed a stronger frontal P2 and parieto-occipital N2 than did nonblinkers at the beginning of the RSVP stream, which might reflect a difference in the attentional response to the stream. The peak amplitudes of the P2s and N2s were separately measured within a time window of 150–240 msec after the onset of the RSVP stream, and independent samples t tests revealed significant (one-tailed) differences between blinkers and nonblinkers for electrodes F7, $t(20) = 2.02$, $SE = .73$, $p = .029$; F8, $t(20) = 2.87$, $SE = .73$, $p = .005$; PO7, $t(20) = -2.15$, $SE = 1.40$, $p = .022$; and PO8, $t(20) = -1.79$, $SE = 1.73$, $p = .045$, but no significant difference for Pz ($p = .175$).

The earlier P3 peaks induced by identified targets suggest that nonblinkers are quicker to consolidate relevant information than are blinkers. Moreover, the differences in FSP amplitudes and the amount of distractor-related activity suggest that nonblinkers are also more efficient in selecting targets from nontargets. An important question is whether consolidation, as evidenced by the P3, occurs earlier in nonblinkers because of differences in speed of information processing or because they more efficiently select targets from nontargets at an early processing stage. If speed of information processing is the only factor differentiating blinkers and nonblinkers, the performance of the two

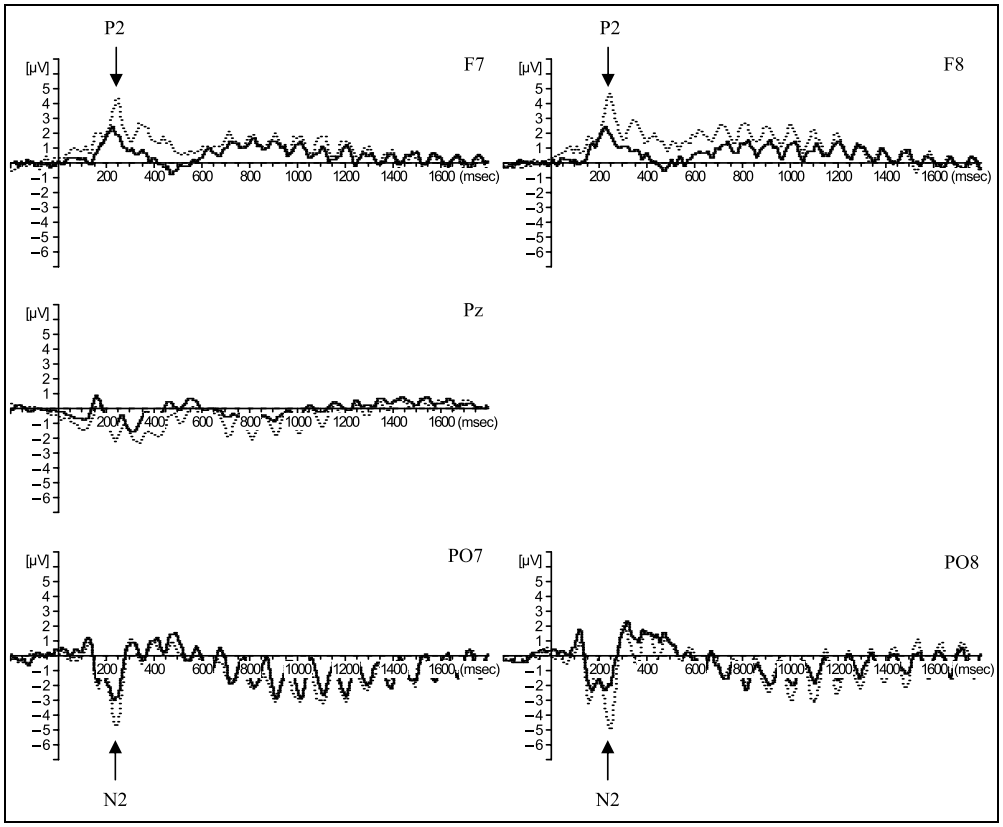

Figure 6. Grand averages of the mean activation at F7, F8, Pz, PO7, and PO8 of nonblinkers (solid line) and blinkers (densely dotted line) as a function of time for no-target trials. ERPs were time locked to the onset of the RSVP stream.

groups should be able to be equated by manipulating the presentation rate of the items in the RSVP stream.

EXPERIMENT 2

If the time available to process information is the limiting factor in the performance of blinkers, increasing the rate of presentation should increase the magnitude of the blink and might also result in an AB for persons identified as nonblinkers. To test the hypothesis that speed of information processing (as indexed by the effects of presentation rate on performance) is the determining factor in the magnitude of the AB, blinkers and nonblinkers were tested by using the same paradigm as in Experiment 1, but with six different rates of stimulus presentation.

Methods

Participants

The same nonblinkers as in Experiment 1 participated in this experiment. The blinker group contained 11 new participants (mean age 21.1 years, 6 women) who showed an AB magnitude of at least 10% in the condition with a 90-msec SOA (see Procedure). Participants received payment of €13 for participating in the experiment, which took approximately 90 min.

Stimuli and Apparatus

The same stimuli and apparatus as in Experiment 1 were used except that the EEG was not measured.

Procedure

The procedure was the same as in Experiment 1, with the following exceptions. The experiment consisted of a practice block of 24 trials and six experimental blocks of 160 trials each. No warm-up trials were provided. A short break was given after each block. Prior to each trial, a fixation cross was presented in the middle of the screen, together with a message at the bottom of the screen prompting participants to press the space bar to initiate the trial. When the space bar was pressed, the message disappeared immediately. The fixation cross remained on the screen for 750 msec. The RSVP stream was presented after 100 msec, and consisted of 14 digit distractors and two letter targets. In the practice block and the first testing block, each item in the stream was presented for 90 msec at the center of the screen. In subsequent blocks of trials, each item was presented for 80, 70, 60, 50, or 40 msec, respectively. The interstimulus interval in all blocks was 10 msec, resulting in stimulus onset asynchronies (SOAs) of 100, 90, 80, 70, 60, and 50 msec. T1 was always presented as the sixth item in the stream. T2 was presented at Lag 1, 2, 3, 4, 5, 6, 7,

or 8. The resulting target onset asynchronies (TOAs) varied depending on the SOA.

Results and Discussion

Figure 7 shows T1 performance as a function of SOA (the interval between successive stimuli) and TOA (the interval between successive targets) for blinkers (A) and nonblinkers (C). A repeated measures ANOVA with group (nonblinkers or blinkers) as a between-subjects factor and SOA (50, 60, 70, 80, 90, or 100 msec), and lag (1, 2, 3, 4, 5, 6, 7, or 8) as within-subjects factors revealed significant effects of group, $F(1,20) = 26.09$, $MSE = 1024.55$, $p < .001$, SOA, $F(5,100) = 72.62$, $MSE = 74.12$, $p < .001$, and lag, $F(7,140) = 57.40$, $MSE = 45.51$, $p < .001$. Only the Group × SOA interaction was significant, $F(5,100) = 5.41$, $MSE = 74.11$, $p = .002$, such that decreasing the duration of stimulus presentation had a bigger impact on T1 performance for the blinkers than for the nonblinkers.

Figure 7 shows performance for T2 on those trials for which T1 was reported correctly (T2|T1), as a function of SOA and TOA for blinkers (B) and nonblinkers (D). A repeated measures ANOVA with group (nonblinkers or blinkers) as a between-subjects factor and SOA (50, 60, 70, 80, 90, or 100 msec), and lag (1, 2, 3, 4, 5, 6, 7, or 8) as within-subjects factors revealed significant effects of group, $F(1,20) = 27.78$, $MSE = 7112.98$, $p < .001$, SOA, $F(5,100) = 79.46$, $MSE = 233.77$, $p < .001$, and lag, $F(7,140) = 14.64$, $MSE = 302.75$, $p < .001$. In addition, all interactions were significant (Group × SOA, $F(5,100) = 4.66$, $MSE = 233.77$, $p = .006$; Group × Lag, $F(7,140) = 8.44$, $MSE = 302.75$, $p < .001$; Lag × SOA, $F(35, 700) = 7.38$, $MSE = 98.33$, $p < .001$, and Group × Lag × SOA, $F(35, 700) = 3.67$, $MSE = 98.33$, $p < .001$). The SOA had a bigger impact on the blinkers than on

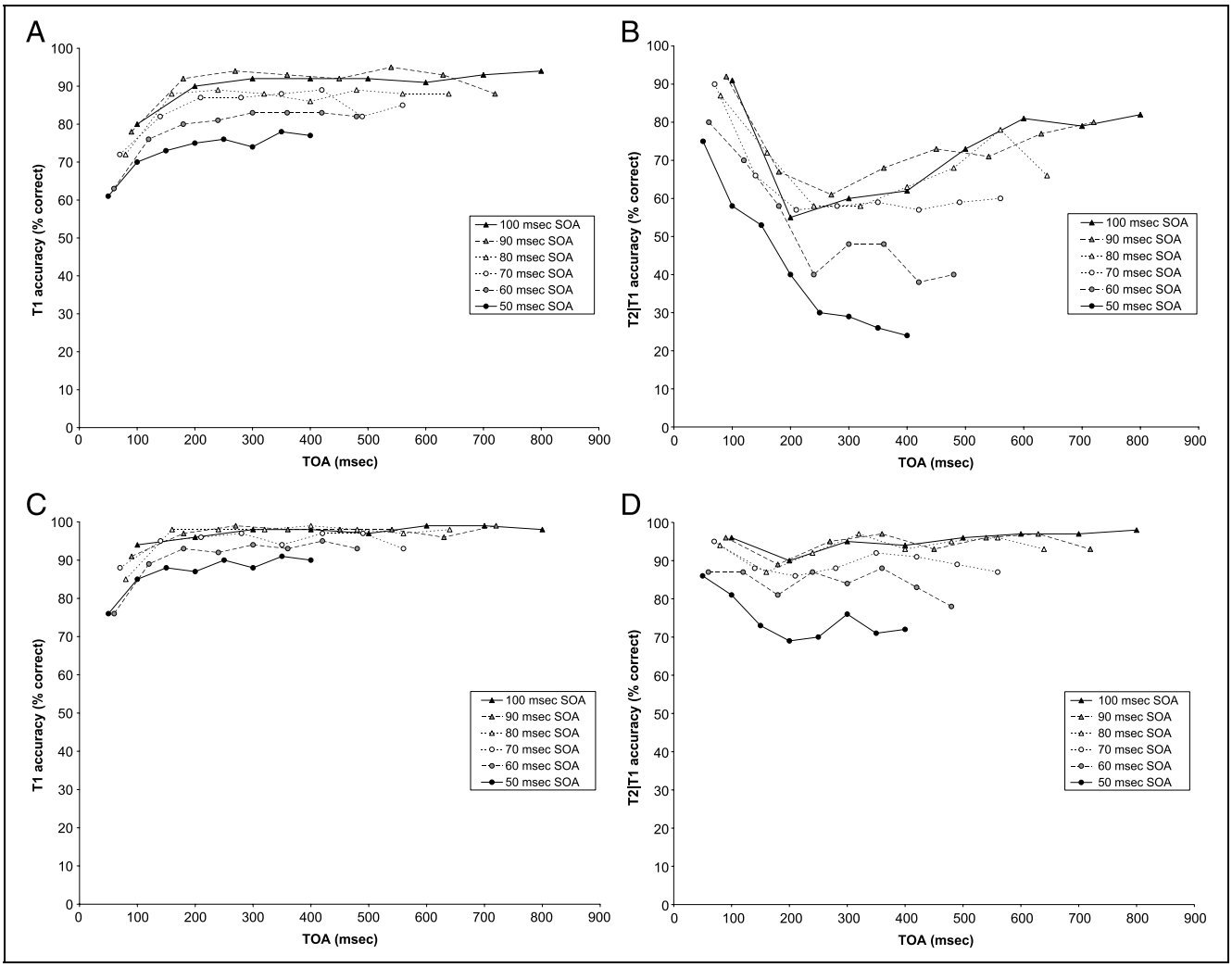

Figure 7. (A) Mean percentage correct report of T1 as a function of SOA (the interval between successive stimuli) and TOA (the interval between successive targets) for blinkers. (B) Mean percentage correct report of T2, given correct report of T1, as a function of SOA and TOA for blinkers. (C) Mean percentage correct report of T1 as a function of SOA and TOA for nonblinkers. (D) Mean percentage correct report of T2, given correct report of T1, as a function of SOA and TOA for nonblinkers.

the nonblinkers, blinkers showed a larger effect of lag than nonblinkers, and the AB increased as the SOA decreased. The three-way interaction reflects that the AB was more strongly affected by SOA for the blinkers than for the nonblinkers.

The magnitude of the AB was calculated separately for each lag ({[(T1 accuracy at Lag n − T2|T1 accuracy at Lag n) / T1 accuracy at Lag n] × 100}) and these values were averaged together. Blinkers showed mean AB magnitudes of 20.8%, 18.4%, 19.2%, 26.1%, 31.5%, and 40.8% for SOAs of 100, 90, 80, 70, 60, and 50 msec, respectively, whereas the mean AB amplitudes for nonblinkers were 2.0%, 2.2%, 3.2%, 5.0%, 5.8%, and 12.7%, respectively. In other words, whereas blinkers showed a clear T2 decrement for all SOAs, nonblinkers showed a T2 decrement of more then 10% relative to T1 only when the SOA was 50 msec.

The AB magnitude did not seem to increase much in the four longest SOAs (100, 90, 80, and 70) for either group. A separate analysis of the blinkers' T2|T1 performance for the four longest SOAs showed a significant effect of SOA, $F(3,30) = 12.87$, $MSE = 230.19$, $p < .001$; lag, $F(7,70) = 9.75$, $MSE = 448.58$, $p = .001$; and a significant Lag × SOA interaction, $F(21,210) = 4.17$, $MSE = 112.24$, $p = .002$. However, visual inspection of Figure 7B shows that although the interaction between lag and SOA was significant, the AB magnitude did not seem to increase systematically as a function of decreasing SOA. Moreover, for the blinkers, the AB seems to be strongest at an TOA of 200–300 msec, regardless of the number of distractors that are presented between the two targets. A separate analysis for the nonblinkers for the longest four SOAs revealed a significant effect of SOA, $F(3,30) = 8.16$, $MSE = 71.76$, $p = .005$, and lag, $F(7,70) = 5.16$, $MSE = 44.48$, $p = .004$. No significant interaction was found, suggesting that shortening the presentation time by 30 msec did not result in an AB for nonblinkers.

These results suggest that the time available to process individual stimuli has little impact on the magnitude of the AB for both groups and therefore cannot fully explain the differences between blinkers and nonblinkers. For nonblinkers, a decrement in T2 performance only seemed to occur at extreme SOAs of 50 and 60 msec. Even when matched according to T1 performance, the nonblinkers still outperformed the blinkers in terms of T2 performance. For instance, the nonblinkers mean T1 performance across lags at an SOA of 60 msec (90.6%) was comparable to the blinkers' mean T1 performance at an SOA of 100 msec (90.7%), $t(20) = .06$, $SE = 2.08$, $p = .96$. In contrast, the nonblinkers' mean T2|T1 performance at an SOA of 60 msec (84.1%) was still significantly better than the blinkers mean T2|T1 performance at an SOA of 100 msec (71.9%), $t(20) = 2.10$, $SE = 5.82$, $p = .049$. Thus, rather than the speed of processing, the efficiency with which targets can be distinguished from nontargets seems to be the crucial factor in determining the magnitude of the AB, and, presumably, the speed with which targets can be consolidated.

GENERAL DISCUSSION

The goal of the present study was to examine individual differences in the magnitude of the AB. Experiment 1 compared the EEG activity of 11 nonblinkers (showing a T2 decrement of less than 10% relative to T1) with that of 11 blinkers (showing a T2 decrement of at least 20% relative to T1). For both nonblinkers and blinkers, distinct P3 components (associated with working memory updating) were found for successfully identified T1s and T2s. For blinkers, no P3 was found for blinked T2s (i.e., when the second target was incorrectly reported or missed; cf., Vogel et al., 1998). Analyses of the P3 latencies revealed that both blinkers and nonblinkers were slower to consolidate T2 than T1, and that they were slower to consolidate the targets when T2 was presented at Lag 3 than at Lag 8. Blinkers were always slower to consolidate targets, especially T2s, than nonblinkers were. These findings replicate previous results by Vogel and Luck (2002), who found a delayed P3 in response to unmasked T2s presented at Lag 3 relative to unmasked T2s presented at Lag 7. We directly compared the P3 evoked by masked but, nevertheless, successfully identified T2s (i.e., nonblink trials) presented at either Lag 3 or Lag 8, and also found that consolidation of T2 is slowed when presented at Lag 3. However, we found a similar consolidation delay for T1. The finding of equivalent Lag 3 consolidation delays for T1 and T2 is problematic for strict bottleneck models of the AB (e.g., Chun & Potter, 1995) and suggests, as discussed below, that interference within VSTM is the locus of the AB effect.

Nonblinkers also showed significant FSP effects over the ventrolateral prefrontal cortex (BA 12/47; electrodes F7 and F8), evoked by successfully identified T1s. In contrast, blinkers showed only a small FSP effect over the left prefrontal cortex and no FSP over the right prefrontal cortex. A significant correlation of −.57 was found between the magnitude of the FSP effect measured over the right prefrontal cortex (F8) and the magnitude of the AB: The more target-related prefrontal activity evoked by T1, the smaller the AB effect.

This correlation suggests that early target-selection processes, presumably originating in the ventrolateral prefrontal cortex (see Smid et al., 1999; Passingham, 1993), may play a crucial role in determining whether or not an AB will subsequently occur. The selection of relevant from irrelevant information determines which information is permitted to enter working memory and conscious awareness. If the selection process is not restrictive enough, reflected by no or little FSP activity, not only targets but also distractors will occupy the limited capacity of working memory, thereby interfering with the further processing of T2.

Additional evidence consistent with this view was provided by the observation that blinkers showed more prefrontal activity than nonblinkers in response to each nontarget presented during the interval in which targets could be expected to appear. The relatively high level of activity in blinkers could indicate that blinkers directed more attention to each nontarget than nonblinkers did (see, e.g., Spitzer, Desimone, & Moran, 1988). In other words, blinkers seemed less able to ignore the distractors than did nonblinkers. Together with the finding of stronger P2 and N2 components at the beginning of the RSVP stream for blinkers compared to nonblinkers, a pattern of results emerges suggesting that nonblinkers might have been less focused on consciously perceiving every stimulus, allowing them to reach ''a more distributed state of attention'' (Olivers & Nieuwenhuis, 2005, p. 10).

The Functional Role of the FSP and SN

It has been suggested that selective attention to visual input involves a distributed network of anterior and posterior brain areas, each supporting a different functional aspect of the selection process (e.g., Smid et al., 1999). Initially, the FSP was thought to reflect a polarity reversal at anterior scalp sites of the posterior SN, both having a common and single posterior source (e.g., Harter & Aine, 1984; Harter & Guido, 1980). However, it has also been suggested that the SN and FSP are related to separate neural mechanisms, as their onset latencies can vary relative to each other (e.g., Kenemans, Kok, & Smulders, 1993; Wijers, 1989), and the SN is sometimes found to be lateralized in conjunction with a symmetrical FSP (e.g., Hillyard & Münte, 1984). Our finding of a dissociation between SN and FSP activity in blinkers and nonblinkers (similar SN activity, but differential FSP activity) supports the idea that the SN and FSP are related to separate neural mechanisms.

The results reported here suggest that adequate SN activity is sufficient for successful identification of T1 (observed in blinkers and nonblinkers), but that prefrontal activity, reflected by a significant FSP (here most clearly observed in nonblinkers) is required to restrict working memory access to targets only, filtering out irrelevant information (i.e., distractors), so that not only T1 but also T2 can be successfully reported even when it is presented at Lag 3. The hypothesis that target-selection processes in the prefrontal cortex, reflected by the FSP, play an important role in determining what information should be selected for admittance to working memory and conscious awareness is consistent with the idea that prefrontal selective mechanisms are crucial for intentional behavior (cf., Passingham, 1993; Näätänen, 1992; Priham & Luria, 1973). According to Passingham (1993), the ventrolateral prefrontal cortex is crucial in selecting nonspatial goals such as conjunctions of color and shape (i.e., objects). Smid et al. (1999) reported evidence suggesting that the SN is associated with a selection-for-perception mechanism, enabling the processing and binding of features, and that the FSP is associated with a selection-for-action mechanism, enabling the selective coupling of relevant stimuli to relevant responses by combining external and internal stimuli (Näätänen, 1992; Allport, 1987).

Interestingly, not only has the ventrolateral prefrontal cortex been specifically implicated in a wide range of cognitive processes, including the selection (Rushworth, Nixon, Eacott, & Passingham, 1997), comparison, and judgment of stimuli held in short-term and long-term memory (Petrides, 1994), as well as holding nonspatial information online (Courtney, Ungerleider, Keil, & Haxby, 1997). The area is also located next to the anterior cingulate (BA 32), the frontopolar cortex (BA 10), and close to the medial prefrontal cortex (BA 9) (see, e.g., Duvernoy, 1999). As described in the Introduction, Feinstein et al. (2004) found that these specific areas were more active in nonblinkers than in blinkers. Combined with our results, the converging evidence supports the idea that the prefrontal cortex plays a crucial role in selecting relevant information from irrelevant information based on an internal target template (Duncan & Humphreys, 1989).

Implications for Theoretical Models of the AB

Although, as shown by the consolidation latencies for blinkers in Table 1, it takes more time to consolidate T2 than to consolidate T1, T1 and T2 consolidation are equally slowed when T2 is presented at Lag 3. According to the two-stage model, the Lag 3 consolidation delay should be considerably longer for T2 than for T1, as T2 would have to wait for T1 to be consolidated before T2 itself can be consolidated. However, this model does not seem to predict T1 slowing at Lag 3. The interference model can account for the slowing of the consolidation of both targets because T1 and T2 are assumed to compete with each other within VSTM, thereby slowing consolidation more or less equally for both targets. The finding that blinkers are slower to consolidate targets than nonblinkers is to be expected if target selection processes are less efficient in blinkers, thereby allowing more distractor information to enter working memory and compete with the targets. This interpretation is consistent with the finding that the blinkers showed more prefrontal activation in response to each distractor than did nonblinkers, suggesting that more distractors may have entered working memory in blinkers than in nonblinkers.

Conclusions

The results of our study strongly suggest that nonblinkers consolidate relevant information quicker than do blinkers, presumably because they are better in

selecting target information at an early stage, thus rejecting distractors more easily and leaving sufficient resources available to report both targets. The amount of target-related activity in the right ventrolateral prefrontal cortex (the FSP at F8) seems a good predictor of the individual magnitude of the AB. We are currently conducting studies to test the generality of the superior selection shown by nonblinkers to explore the relation between basic cognitive operations and the ability to process the varied sorts of information encountered in daily life.

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